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Arthropods: A Convergent Phenomenon

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INTRODUCTION

"In the absence of precise knowledge of the meaning of animal shapes it has been safe to put forward many unsound comments on arthropod evolution" (Manton, 1958, p. 64). Thus we can characterize the nature of the revolution in our understanding of arthropod functional morphology and embryology which has taken place in the last generation. We have moved from a condition in which many gaps in our knowledge of basic arthropod biology existed, but which never deflected people from engaging in extensive phyletic speculation. We are now arriving at a phase in which a wide range of investigations of basic form and function, what Beklemishev (1969) refers to as "promorphology," are forcing us to re-evaluate traditional views of arthropod evolution. A long-established monophyletic viewpoint is giving way to a polyphyletic one. However, as the historical review of Tiegs and Manton (1958) reveals, the pendulum of debate of monophyly *versus* polyphyly in arthropods has been swinging for some time.

Recent functional morphological and comparative embryological studies on modern groups of arthropods reveal that we are dealing with several coherent taxonomic groups of the status of phyla. Using this information, as well as paleontological evidence, integration of the trilobitomorphs and pycnogonids into this scheme is

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attempted. There are seen to be at least three, probably four, phyla which have reached the arthropodous grade of organization: Uniramia, Crustacea, Cheliceriformes, and probably Trilobitomorpha.

It is my intent to review and summarize some of these recent discoveries in comparative arthropod biology which have occurred since Tiegs and Manton (1958). I will also evaluate what is known of some of the "peripheral" groups which are not as well understood as the major living groups (trilobites and pycnogonids) to see where they might fit in any phyletic arrangement of the arthropods.

CONVERGENT PHENOMENA

The central dominating theme of arthropod evolution is the multiplicity of convergent development. *No* phyletic scheme, monophyletic or polyphyletic, can escape this (Tiegs and Manton, 1958). In the late 1800's the arthropods were viewed as a tightly organized group. The merostomes were considered to be Crustacea. The arachnids were aligned with the myriapod-hexapods in the Tracheata, based on the possession of tracheae in many of these animals. The presence of Malpighian tubules in insects and many arachnids served to strengthen the links between these two groups. But Lankester (1881) effectively demonstrated the affinities of *Limulus* with scorpions and thus all arachnids. The Chelicerata were established as a group separate and distinct from all others. The arachnids, with their tracheae and Malpighian tubules, were seen to be derived from marine merostome types and not myriapodous forms. Later, study of Malpighian tubule development revealed that these structures were evaginations of the proctodeum or hindgut, i.e., ectodermally derived, in the insects, and outgrowths of the midgut, i.e., endodermally derived, in arachnids. The original convergence of these excretory structures demanded by taxonomic considerations of external anatomy of Chelicerata were eventually reinforced by embryonic studies.

Subsequent to the elucidation of the Chelicerata, the crustaceans and myriapod-hexapod groups were allied in the subphylum Mandibulata (Snodgrass, 1938), but the recent work of Manton (1964) on the functional morphology of arthropod jaws has completely altered our understanding of mandible evolution.

There are two basic jaw types in arthropods: a gnathobasic type, in which only the modified coxa is used for biting; and the whole-limb type, in which the entire appendage is employed, the biting sur-

face being the tip of the distalmost segment or distalmost part of the whole limb jaw. The gnathobasic type is found in the crustacean mandible (and on the prosomal appendages 2 to 6 in *Limulus*). The whole-limb jaw is used in the onychophorans, myriapods, and hexapods. Manton (1964) concluded that these jaw types are so distinctive that neither one can have given rise to the other.

Within each basic jaw type there are different modes of action. The gnathobasic jaw of Crustacea primitively employs the coxal promotor-remotor muscles to produce the antero-posterior rolling action of the molar process around a dorso-ventral axis. In some eumalacostracans the development of an incisor process posterior to the molar process produces a secondary transverse action using the incisor process. Powerful remotor muscles produce the grinding (rolling) action of the molar process and the biting (transverse) action of the incisor. The weaker promotor muscles part the molar and abduct the incisor processes.

The living merostomes, sometimes placed in three separate genera (*Limulus*, *Carcinoscorpius*, and *Tachypleus*), use prosomal appendages 2 to 6 as both walking limbs and biting limbs. The coxae on these appendages are capable of two different actions. A series of promotor-remotor muscles moves the coxa antero-posteriorly when the animal walks. Another set of special abductor-adductor muscles moves the coxa transversely when the coxa is used for biting. Manton claims that the muscles used and the modes of action of the crustacean and limulid gnathobasic jaws are so different that there is little possibility that they are related in any way to each other and are therefore only analogous.

The whole-limb jaw type also exhibits different modes of action. The onychophoran mandible has an antero-posterior slicing action, each jaw frequently moving in opposite phase to the other, like the onychophoran walking legs. Some hexapods have a rolling, grinding action similar to crustaceans. The basic promotor-remotor action in hexapods can also be converted in some forms to a transverse action with the development of incisor processes. As occasionally happens in the eumalacostracans, the hexapods, especially pterygote insects, greatly reduce the anterior molar process and completely convert the mandible to a transverse type while still employing promotor-remotor muscles.

The segmented mandibles of myriapods have a transverse action with the musculature being largely adductor, the abduction being

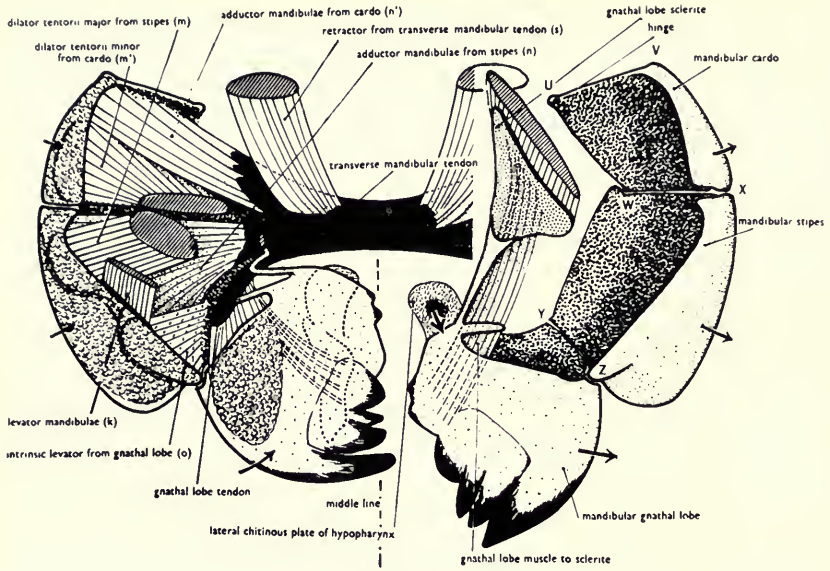


FIG. 1. Anterior view of the mandibles of the diplopod, *Poratophilus punctatus*. *Left:* the musculature is entire and the mandible is in a position of maximum adduction. *Right:* muscles are removed from the mandibular cuticle, with the exception of one intrinsic muscle, and the mandible is in a position of extreme abduction. (From Manton, 1964.)

achieved indirectly. Powerful adductor muscles inserting on the cardo, stipes, and gnathal segments of the mandible exert a strong force (fig. 1). Abduction is achieved by the endoskeletal tentorium which swings downward and forward from the inner surface of the cranium and pushes the jaws apart. This is a basic arrangement for all myriapod groups and is so different from that of the hexapods that neither can have given rise to the other. Manton (1964, 1969) thus disproves the view that insects have been derived from symphylans as has been commonly suggested in the past; and Rasnitsyn (1976) agrees based on a consideration of fossil evidence.

The old arthropod subphylum Mandibulata is thus seen to have no basis (fig. 2). Similarities between crustaceans and myriapod-hexapods are merely convergent. Though the variations in jaw function between Myriapoda and Hexapoda are striking, there remain a great enough number of similarities shared by all classes, such as the labrum, derivation of the jaw, a single pair of antennae, tracheae, and manner of potential entognathy (though this has arisen several times within the myriapod-hexapod group), that it appears that the onychophorans-myriapods-hexapods form a fairly coherent unit.

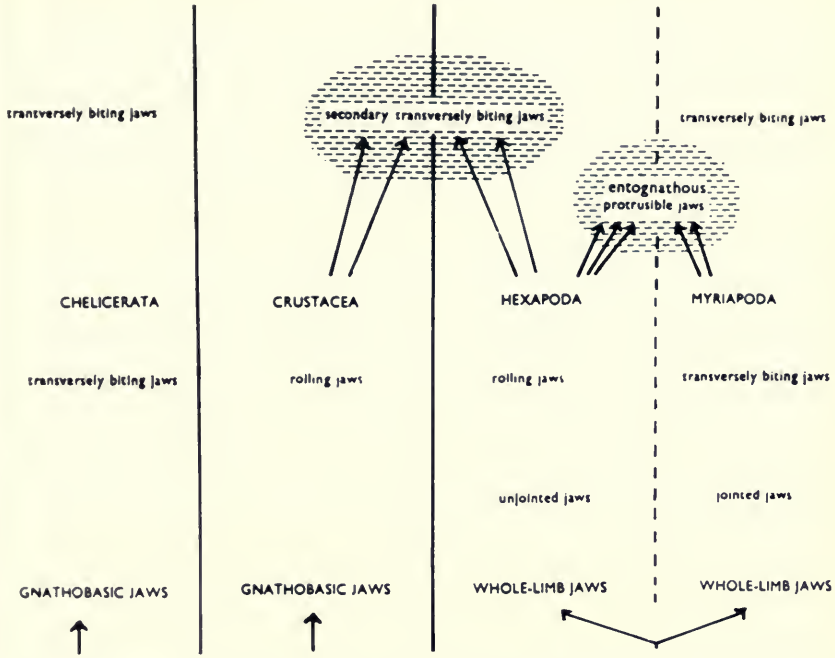


FIG. 2. Diagram showing the conclusions reached concerning the distribution of the principal types of mandibles or jaws (below) and the derivation of the jaw mechanism (above). Heavy vertical lines indicate an absence of common ancestry between the jaws referred to on either side; an interrupted vertical line indicates separate evolutions of jaw mechanisms which probably had a common origin; the shaded area indicates jaw mechanisms showing convergent similarities derived from unlike origins. (From Manton, 1964.)

When the concept Mandibulata is discarded, another striking convergence is revealed: that of compound eyes. Recent work has indicated differences in the pigment screen between crustacean and insect compound eyes (Struwe et al., 1975), and there is a lack of homology between insect primary pigment cells and crustacean corneagen cells (Elofsson, 1970) as has been previously supposed. Elofsson (pers. comm.) believes insect and crustacean compound eyes to be as different from each other as are vertebrate and cephalopod eyes, i.e., a striking gross superficial similarity exists, but constituent parts have quite different embryonic histories. Compound eyes are also possessed by merostome chelicerates and trilobites. The compound eyes of *Limulus* have a thick cornea covering over all the ommatidial units, in the living limulids as well as the fossil merostomes, as opposed to the typically distinct cornea over each

ommatidium in the eyes of crustaceans and insects. Little is known about the trilobite eyes that can be effectively compared with the detail available in living arthropod eyes. Though trilobite compound eyes are composed of several optical units (Clarkson, 1973) some may not have been as closely aligned and co-ordinated as those of living arthropods (Clarkson, 1966). Several different types of trilobite eyes are recognized (Clarkson, 1975; Jell, 1975).

It may be difficult to accept the convergent development of such a complex and important structure as the compound eye, yet I think this convergence is probably no more profound than that which occurs between the eyes of some cephalopods and vertebrates. Arthropods being what they are, with the ocellus representing the simple basic optical unit, there is only a certain optimal way to solve the problem of visual perception. The ocellus is common to all groups of arthropods and given this simple structure as a foundation, natural selection has resulted in compound eyes in various sorts of crustaceans, insects, trilobites, and merostomes.

LEG ANATOMY

In addition to a uniformity in jaw apparatus, the onychophorans-myriapods-hexapods share a common uniramous appendage. This appendage evolved in a condition where a long series of identical limbs had to be precisely co-ordinated to achieve locomotion. Lack of co-ordination would lead to interference of one limb with an adjacent one and stumbling (Manton, 1969).

Body shape of the various groups within this assemblage—named the Uniramia by Manton (1973a)—is correlated with habit. The onychophoran unsclerotized, deformable body, connective tissue endoskeleton, and unstriated muscle enables these animals to squeeze through narrow openings and spaces, allowing them to escape predators; though some might prefer to continue to use these same characters as criteria for maintaining Onychophora as a separate phylum. The diplosegments of the Diplopoda are related to a need to develop motive force in burrowing or pushing through leaf litter, soil, and decomposing wood. In the Chilopoda the lengthening of the legs, variation in body segment size, and special muscle insertions enable these animals to exploit a running, carnivorous habit. The Sympyhla have divided tergites which allow them to twist and flex their bodies in climbing under, over, around, and in between obstructions and in executing sharp angle turns to escape and elude

predators. The Hexapoda have reduced the number of legs, lengthened the appendage, and spread out the field of movement of each limb (with resultant increase of mechanical advantage) to allow them to exploit the resultant versatility of movement and speed.

The chelicerates developed from long-legged forms with few appendages on the body and no more than five postoral limbs on the adult prosoma (Manton, 1973a, b). There is no necessity to rigidly co-ordinate movements among such a small number of legs and so chelicerates consequently execute rather inaccurate stepping movements in contrast to the Uniramia. In arachnids the stepping movement does not typically involve a promotor-remotor swing of the coxa. Rather, the chelicerates employ a "rocking" action in lengthening the stride of the leg to greater effect than any other arthropods. This motion is so termed from the position of the dorsum of the appendage during movement: on the propulsive backstroke, the dorsum is directed forward; on the recovery stroke, when the leg is brought forward, the dorsum is directed posteriorly. The appearance of a single isolated leg would then describe a rolling or rocking motion. Manton (1973b) is not clear on just how this rocking is achieved, but Schram and Hedgpeth (1978) note similar movements in pycnogonids and attribute it in part to sets of adjacent but separate extensor muscles in the basalmost segments of the legs.

The primitive living crustaceans have a flat, multi-ramous appendage (Hessler and Newman, 1975) which is used in a metachronal, swimming pattern. The legs are directed ventrally, under the body, and locomotion is typically combined with food getting and processing.

This multiplicity of jaw structure and embryonic derivation, combined with a meticulously detailed analysis of leg movements compelled Manton (1973a) to view arthropods as a grade of evolutionary organization containing three phyla having independently arrived at this grade: Uniramia, Crustacea, and Chelicerata. The uniramians evolved from multi-legged, uniramous, soft-bodied or flexible forms with lobopodial appendages that handled food at the appendage tips. Manton is less clear about what the ancestors of the crustaceans and chelicerates were like than she is about the uniramians, but we may infer that the crustaceans would have evolved from multi-legged, polyramous forms with foliaceous (leaf-like) appendages directed ventrally that handled food at the leg bases. The chelicerates would be developed from possibly uniramous forms, with few legs, possibly processing food at the leg bases.

ARTHROPOD EMBRYOLOGY

An independent set of data from that of Manton (1973a), with perhaps more convincing reasons for recognizing three arthropodous phyla, comes from the comparative embryological studies of D. T. Anderson (1973). His findings (fig. 3) for Annelida, Uniramia, Crustacea, and Chelicerata are summarized in Table 1. Data on the Pycnogonida has been added from T. H. Morgan (1891), Dogiel (1913), Sanchez (1959), and King (1973).

The uniramians and annelids are seen to have a basic similarity of development. The annelids have spiral cleavage in eggs with little to moderate amounts of yolk (while uniramians do not exhibit spiral cleavage because of a modification induced by large amounts of yolk in the egg). In annelids the presumptive endoderm (midgut) arises from the 3A, 3B, 3C, and 4D cells located along the ventral part of the blastoderm. This midgut area is enclosed by an overgrowth (epiboly) of cells from the dorsal blastoderm. The stomodeum arises from the 2b cell at the time of gastrulation as a solid mass of cells which subsequently hollows out and forms a mouth. The presumptive mesoderm arises from the 4d lineage, is located *posterior* to the presumptive endoderm, and becomes internalized during the epiboly of the ectoderm. The mesoderm then grows forward as a pair of bands from which the somites bud. The presumptive ectoderm of the embryo develops from the 2d lineage.

The uniramians have a developmental pattern like that of the annelids, although cell lineages cannot be traced because of the loss of spiral cleavage. The presumptive endoderm is a group of cells on the ventral surface of the blastomeres. (Frequently large anterior and smaller posterior midgut sections can be delineated, as in the Onychophora.) Gastrulation typically occurs with the presumptive endoderm migrating inward and becoming vitellophagic. The stomodeum forms a solid mass of cells which then hollows out as a tube. The presumptive mesoderm in the onychophorans and chilopods arises from an area posterior to the presumptive endoderm (in the same position as in the annelids) and after involution, grows forward as a pair of bands. The annelid and uniramian development can thus be seen to conform to a basic plan. The uniramians, however, are primitively epimorphic in their development, i.e., hatching with the adult complement of segments.

The crustaceans are entirely and strikingly different from the above pattern. The cleavage of crustaceans which can be followed

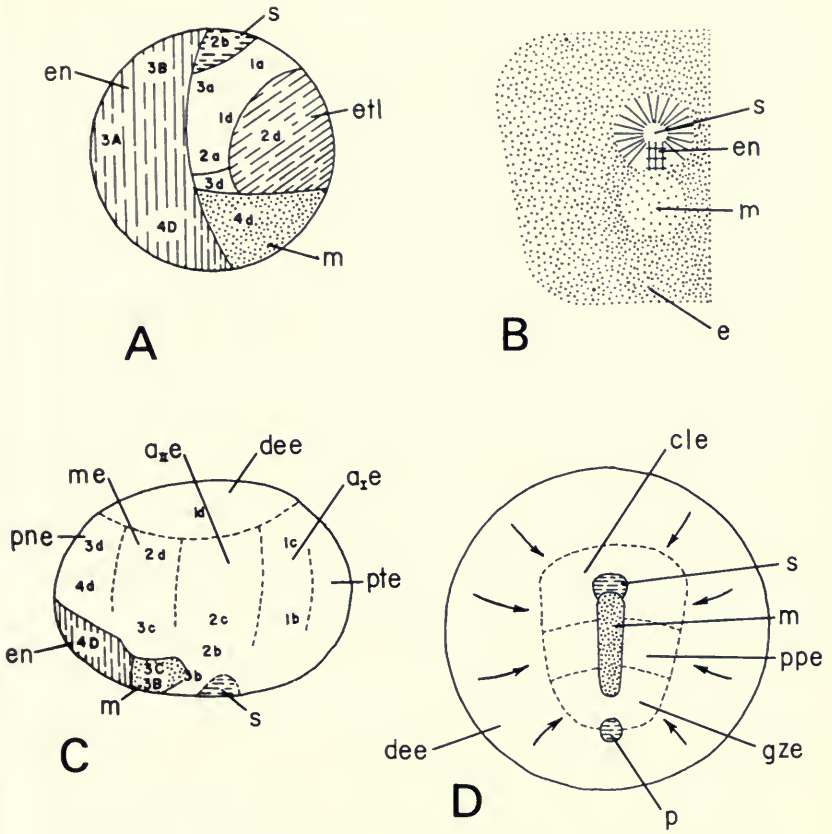


FIG. 3. Blastoderm fate maps of various types of articulates. **A**, the annelid, *Tubifex*; **B**, the onychophoran, *Peripatus*; **C**, a cirriped crustacean; **D**, a xiphosuran chelicerate. s=stomodeum, en=endoderm, m=mesoderm, e=ectoderm, etl=ectodermal teloblasts, pne=postnaupliar ectoderm, me=mandibular ectoderm, $a_{II}e$=antennal ectoderm, a_Ie=antennulary ectoderm, pte=protocerebral ectoderm, dee=dorsal extraembryonic ectoderm, cle=cephalic lobe ectoderm, ppe=pedipalp ectoderm, gze=growth zone ectoderm, p=proctodeum. It is important to note the relationships between the stomodeum, endoderm, and mesoderm. (From Anderson, 1973.)

out is spiral and can allow the tracing of cell lineages. The presumptive endoderm arises from the 4D cell only. The presumptive mesoderm arises from the 3A, 3B, and 3C lineages and is thus *anterior* to the presumptive endoderm, rather than posterior as in the uniramians and annelids. The presumptive ectoderm arises from the 3d and 4d cells and is very early zoned into regions conforming to the nauplius topography. The stomodeum arises from the 2b cell, but does so independent of gastrulation. Thus the presumptive area relation-

TABLE 1. Comparison of early embryonic conditions in various groups of arthropods.

	ANNELIDA	UNIRAMIA	CRUSTACEA
CLEAVAGE	spiral	non-spiral	spiral
STOMODEUM	2b arises as solid mass of cells at time of gastrulation	invaginates as solid mass at gastrulation, seals off, and forms tube and mouth	2b independent of gastrulation
PRESUMPTIVE ENDODERM	3A, 3B, 3C, and 4D	midventral sheet of surface cells	4D
PRESUMPTIVE MESODERM	4d posterior to presumptive endoderm	surface cells posterior to presumptive endoderm region	3A, 3B, and 3C anterior to presumptive endoderm
PRESUMPTIVE ECTODERM	2d ectoteloblast ectoderm	bilateral, ventral bands lateral to presumptive endoderm	3d and 4d postnaupliar ectoderm
COMMENTS	mesoderm proliferates anteriorly as paired bands	mesoderm proliferates anteriorly as paired bands only in primitive forms	

ships in the crustacean blastoderm are quite different than that seen in the uniramians. The Crustacea have anamorphic development, typically undergoing a more or less extensive larval phase after hatching.

Chelicerate embryology has not received the attention that other arthropod groups have, but from what is known, the chelicerates do not have spiral cleavage. The cleavage is total, however, despite the amount of yolk present. The presumptive endoderm is segregated internally during cleavage. Typically the egg divides completely. Then the nuclei and surrounding cytoplasm "float" to the surface of

CHELICERATA	PYCNOGONIDA		
	little yolk	moderate yolk	copious yolk
non-spiral	non-sprial, but with distinct macro- and micromeres		
associated with presumptive mesoderm at anterior end of gastric groove			associated with presumptive mesoderm
segregated internally during cleavage- some groups with multipolar delamination of vitellophages	dorsal cell sinks and proliferates, or multi-polar delamination from the endoderm	dorsal macromeres enveloped by ventral micromeres	multi-polar delamination from blastoderm of at least vitellophages
midventral cells which form a gastric groove that sinks and proliferates	circum-presumptive endoderm cells sink and proliferate or delaminate (?)	delaminates from edge of micromere cap	delaminates from circumstomodeum region
circum-preaumptive mesoderm and zoned	superficial ventral cells	ventral micromeres	micromere forming blastodisc
mesoderm sinks at gastric groove and proliferates outward between ectoderm and endoderm	little work done, and that sometimes contradictory in details		

the developing embryo, and begin to divide and develop a cell layer around the yolky cells on the inside. The presumptive mesoderm exists as a small, elongate area along the ventral midline of the blastodisc. The mesoderm sinks inward as a gastric groove and proliferates cells that spread outward between the ectodermal and endodermal layers. The stomodeum is associated with the presumptive mesoderm at the anterior end of the gastric groove and forms the mouth at the time of mesoderm initiation. The embryonic ectoderm occupies the rest of the germinal disc and is zoned in patterns corresponding to the first four postoral embryonic segments. Nothing

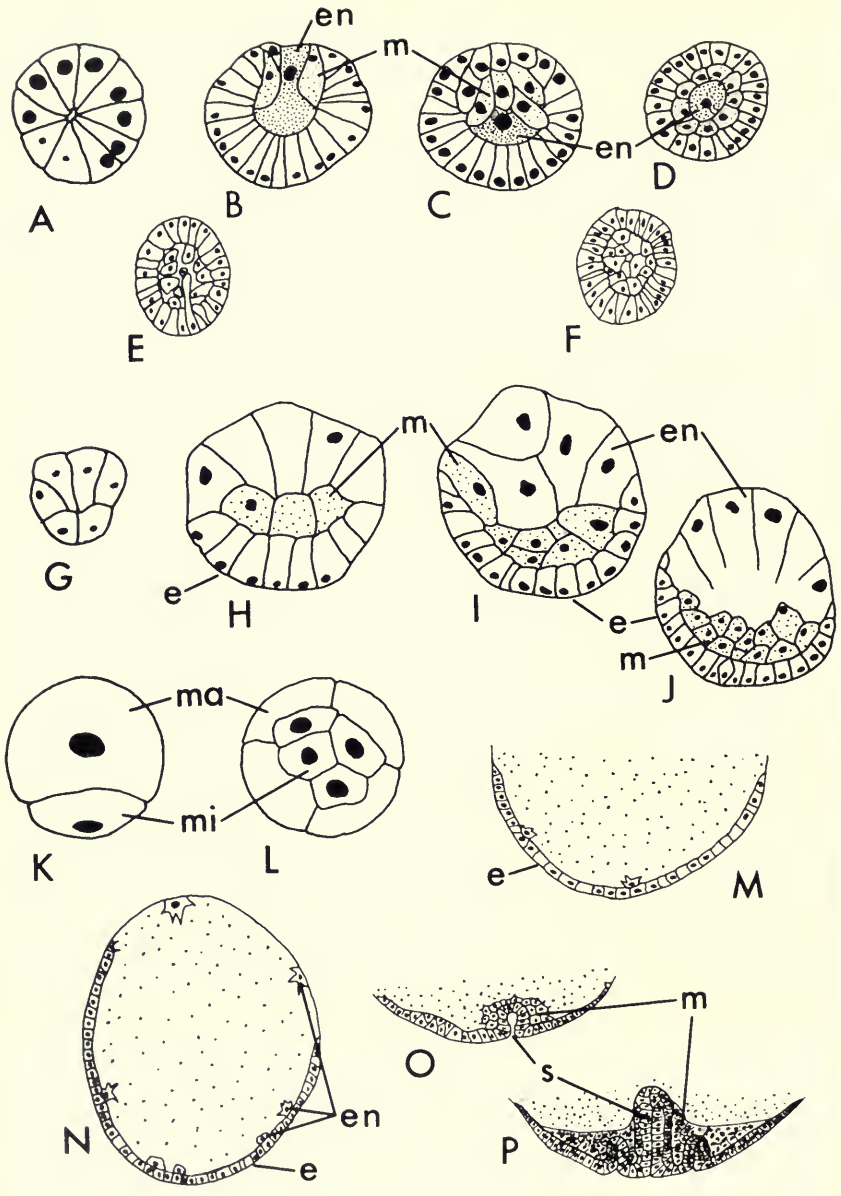


FIG. 4. Early embryology of pycnogonids. **A-D**, *Phoxichilidium* (from Dogiel, 1913); **E, F**, *Tanystylum orbiculare* (from Morgan, 1891); **G-J**, *Nymphon* (from Dogiel, 1913); **K-P**, *Callipalene empusa* (from Morgan, 1891). e=ectoderm, m=mesoderm, en=endoderm, ma=macromere, mi=micromere, s=stomodeum.

can be determined concerning cell lineages in chelicerates (or if they indeed ever had any). Certain features of their development allow them to be separated from other arthropods, viz., the simultaneous separation of presumptive endoderm from other regions with cleavage, the initiation and sinking of mesoderm by delamination along the ventral midline of the embryo. Chelicerates have epimorphic development.

It is unclear where Pycnogonida fit into this embryonic scheme; Anderson (1973) did not deal with them. Little reliable work has been done on pycnogonid development. A short review of what is known from the literature is attempted here (fig. 4). Their cleavage is total and non-spiral. Sanchez (1959) claimed to detect a spiral arrangement in the eight-cell stage of *Callipallene.* Morgan (1891), however, indicated cell lineages in *Callipallene* could not be traced and that the "micromeres" in such an arrangement are the only cells which eventually form the germinal disc. The yolk in pycnogonids can range from small to large amounts and the patterns of the presumptive areas in the blastoderm vary among forms with different amounts of yolk. In the eggs with little yolk, the presumptive midgut forms from a surface cell which sinks to the interior and proliferates to form a syncytium (Dogiel, 1913). The mesoderm in such forms develops from cells which surround the presumptive midgut cell and delaminate mesodermal cells at the time the endoderm differentiates. Morgan (1891) reported multi-polar delamination of the endoderm in the pycnogonids with little yolk that he studied, *Phoxichilidium maxillare* and *Tanystylum orbiculare,* and is unclear as to how the mesoderm developed in these forms.

In pycnogonids with moderate amounts of yolk, such as *Nymphon stromii,* the presumptive midgut develops from dorsal "macromere cells" of the embryo which come to be enveloped by an overgrowth of ventral "micromere cells." The presumptive mesoderm arises from some cells around the edge of the micromere "cap" which, when the "blastopore" reaches the equator of the embryo, migrate in under the micromere cap and proliferate mesoderm. Dogiel (1913) is unclear as to whether this is a true migration of cells or a marginal delamination from the micromere cap.

In forms with large amounts of yolk, like *Chaetonymphon spinosum* or *Callipallene empusa,* the division of the "macromere" cells stops at an advanced stage (cytokinesis is typically incomplete in many of these cells). Only the micromeres continue to divide, spread

over the yolky macromeres, and form a germinal disk (Morgan, 1891). Cells which form the endodermal tissue arise by multi-polar delamination from the disc. The mesoderm arises by multi-polar delamination of cells from around the region of the involuting stomodeum.

The presumptive ectoderm of all pycnogonids is zoned into five regions and soon gives rise to the ventral organs corresponding to the protocerebral brain and first four postoral embryonic ganglia. Many pycnogonids have epimorphic development, though some of them are anamorphic with a protonymphon larva.

The precise affinity of pycnogonids based on what is known of their embryology is inconclusive. The early separation of the endoderm during cleavage, the association in at least some of the pycnogonids of mesoderm formation with developing stomodeum, and the zonation of the ectoderm suggests perhaps at least distant relationship with the chelicerates. But a great deal more conclusive information is needed, especially on the forms with large amounts of yolk in the egg, before pycnogonid embryology can be co-ordinated with that of other arthropods.

TRIPHYLY *versus* DIPHYLY

A modification of the phyletic scheme of Manton and Anderson has been proposed by Cisne (1974, 1975) as a result of his examination of the internal anatomy of trilobites. Cisne used stereoscopic x-ray techniques to study some unusual preservations high in pyrite of *Triarthrus eatoni.* He obtained information on trilobite internal soft anatomy unknown before, and was able to discern appendage structure, digestive organs with extensive diverticula in the cephalon, and the body and appendage muscles. Further, he found that the body muscles conform to a pattern found in the cephalocarid crustaceans (Hessler, 1964) and this reinforced Cisne's (1973) idea that trilobites and cephalocarids were structurally and functionally similar in their feeding habits. Cisne is very unclear, however, as to specific details in this conception. This muscular similarity he takes as proof that these two groups are related and thus proposes a diphyletic scheme for the arthropods (Hessler and Newman, 1975, concur). On one hand are the Uniramia and on the other are the Trilobita-Crustacea-Chelicerata. Neither Cisne nor Hessler and Newman comment on Anderson's (1973) crucial embryological studies of the chelicerates and crustaceans nor on Manton's (1973b) observa-

tions on chelicerate appendage morphology and derivation. There are serious problems concerning Cisne's (1974, 1975) supposed similarities in trilobite and primitive crustacean feeding habits and with his views of embryology which will be taken up below.

The continuing problem among arthropodologists now seems to be not so much that the assemblage may be polyphyletic, but rather how many times this arthropodous phenomenon was evolved into, especially in regard to the trilobite-crustacean-chelicerate-pycnogonid branch. I will attempt to present below an examination of the available evidence that might serve to clarify the inter-relationships of these marine arthropods.

LARVAL SEGMENTS

Anderson's (1973) treatise, while doing a superb job on the arthropod groups he covers, does not discuss the pycnogonids and the trilobites. As was stated above, what little is known of pycnogonid development is frequently not reliable nor very helpful in revealing their relationships, and although trilobites can never be known in the detail of living arthropods, some gross factors of trilobite development are known.

Excellent reviews of trilobite development have been assembled by Whittington (1957, 1959). Trilobites are anamorphic with the protaspis as the earliest larval stage recognized (fig. 5). Some students have questioned whether the protaspis is indeed the earliest phase in the developmental sequence of the trilobites. It is suggested that some unfossilized pre-protaspis stage may have existed. (Gurney suggested in 1942 that nauplii evolved from them.) This is, of course, a possibility, though the size of protaspids, 0.25-1.0 mm., would suggest that at the very least we are dealing with a stage very close to that which hatched from an egg. Apparently not all protaspids were fossilized, the protaspids of the primitive olenellid trilobites have never been found. Sclerotization of the earliest stages in trilobite development may have been a relatively late evolutionary event. Many of the larger types of protaspids, those in excess of 0.4 mm., have the axis divided into five rings. (Smaller protaspids show no sign of this division.) The most anterior ring is the largest, is associated with the eyes, and possibly represents an acron. The remaining four segments, ending in the occipital, have been interpreted as the basic four segments of the adult trilobite cephalon (Henricksen, 1926; Beklemishev, 1969). This axial segmentation of

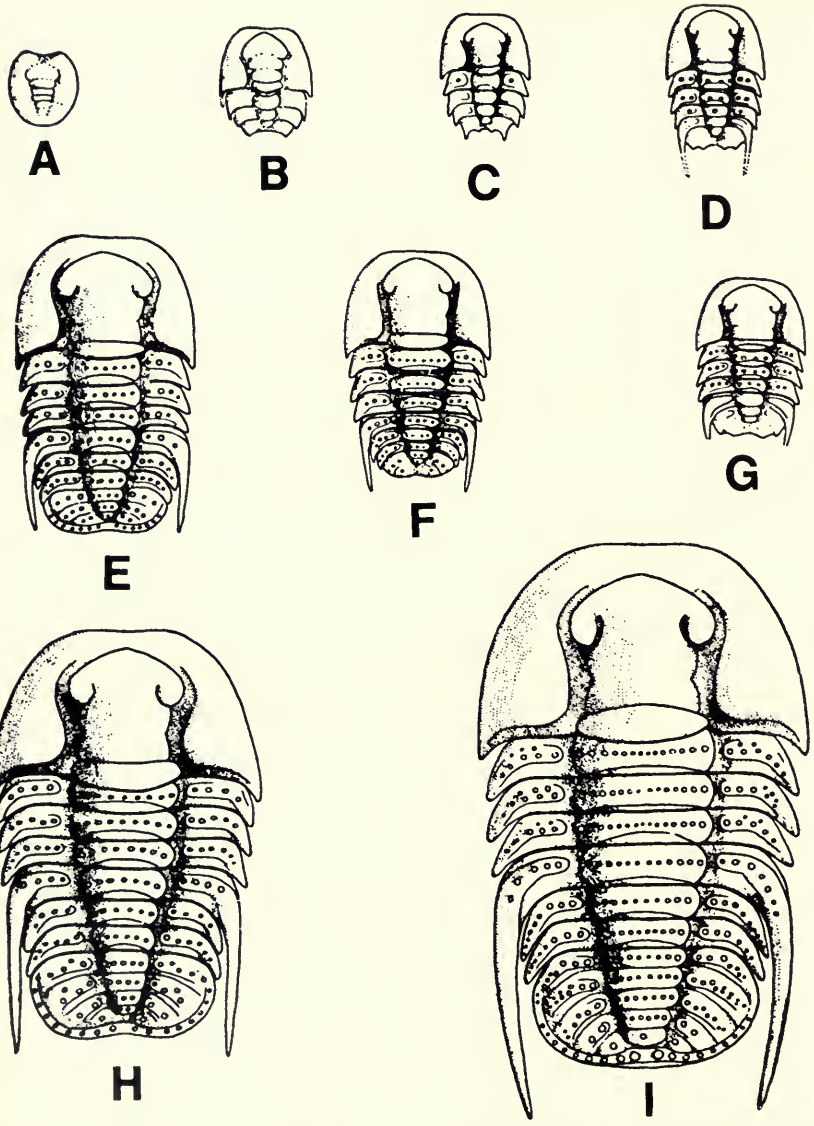


FIG. 5. Anamorphic larval stages of the trilobite *Shumardia pusilla.* A, protaspis; B-G, meraspis, degrees 0-5; H, I, holaspis stages. (From Whittington, 1959.)

the protaspid is frequently lost in the higher trilobites, e.g., in the Lichidae (Whittington, 1956) the protaspids have no segmental grooves but have five sets of spines thought to correspond to the five basic axis segments.

Trilobites have been frequently linked phyletically to merostomes. Iwanoff (1933) suggested the development of *Tachypleus* indicated a phyletic relationship with the trilobites. Iwanoff rejected the so-called "trilobite larva" of the limulids as indicating a relationship of the two groups (he suggested the larva was more like the Carboniferous merostome *Euproops* than a trilobite). His chief reason for relating the two groups was that in *Tachypleus* the initial delineation of body segments by the mesoderm is into four somites, and he compared these to the four "post-acronal" segments of the trilobite protaspis.

This segmental arrangement is similar to that of the pycnogonids. In these arthropods the ectoderm produces five ventral organs which eventually give rise to the protocerebral (acronal) part of the brain and the first four embryonically postoral ganglia. In those pycnogonids which have a protonyphon larva, the first three of these ganglia are associated with the chelifore, pedipalp, and oviger segments respectively—the last ganglion not being associated with any appendages at this stage.

The crustaceans, however, have a different embryonic segment pattern all together. In the initial nauplius stage typically three ganglia and three sets of appendages appear: the antennules, innervated by the deutocerebral portion of the brain, and the antennae and mandibles, innervated by the first two postoral ganglia. Anderson (1965, 1967) and Sollaud (1923) document variations in numbers of ganglia, but it is not clear if these are not secondary.

It would seem that trilobites, chelicerates, and pycnogonids all share early developmental stages with four postoral segments, while the Crustacea seem to be quite distinctive with only two. Whether the trilobites have the *earliest* "embryonic" stage with four postoral segments, as in the chelicerates and pycnogonids, is not at all determinable. Melnikov (1974) feels all arthropods have the same number of larval segments, but reasons largely in hypothesized stages.

BRAIN ANATOMY AND HEAD SEGMENTS

This consideration of embryonic larval segments in arthropods brings us to what Manton (1949) calls the "vexed subject" of head segmentation. Myriad interpretations by various authors have been put forward from time to time (for recent summaries see Manton, 1949; Bullock and Horridge, 1965; Beklemishev, 1969). Hedgpeth

(1954) termed these efforts as "the amiable pastime of phylogenetic arboriculture."

All these efforts to determine the primitive number of head segments have been based for the most part on embryos (Manton, 1960). Manton (1949), however, pointed out some principles of embryology which are typically ignored in such speculations: 1) Somite boundaries are obvious, but two connected or separate coelomic sacs are not conclusive evidence of two somites. 2) Somites can be united to form one unit, but the early development usually shows evidence of such a fusion. 3) Coelomic sacs can arise from several mesodermal lacunae in a somite (especially in large embryos) and such lacunae do not indicate multiple somites. Her opinion was that most of the schemes of head segment homologies were probably not to be taken too seriously.

The homology of head segments is necessarily related to the homology of brain regions. Bullock and Horridge (1965), after reviewing the literature, opted for the simplest, most parsimonious arrangement they could come up with, and which would permit a correspondence of nerve roots to similar regions in all arthropod groups and the annelids. This sort of approach was developed and is used in vertebrate morphology, is certainly more pragmatic, and may be more logical. If we are, in fact, dealing with separate phyla, it may be unreasonable to demand the homology of all head structures. Using this scheme, the anteriormost appendages of arthropods can be compared (table 2). Manton (pers. comm.) would disagree in principle with Bullock and Horridge.

Bullock and Horridge considered the protocerebrum and deutocerebrum to be two parts of an asegmental anterior neural mass (acronal). (There seems to be some embryonic indication that there may be true somites in the preoral region (Manton, 1960). Thus the term "acronal" here may be misleading.) The tritocerebrum is the first in the postoral series of ganglia. Pycnogonids and chelicerates do not have a deutocerebrum. The Crustacea and Uniramia are the only groups with true preoral (possibly acronal) appendages.

The trilobite cephalic condition is only beginning to be made clear. Cisne (1974) records four somites in the cephalon of *Triarthrus*, an antenna-bearing segment and three leg-bearing segments. He claims that the antennal segment is preoral in derivation. Cisne homologizes this segment with the cheliceral segment of the chelicerates, but he mistakenly claims that this segment is preorally derived in

TABLE 2. Topological comparisons of appendages in various arthropodal groups based on neural innervation scheme of Bullock and Horridge (1965). Trilobites based on data of Cisne (1974). Only the anteriormost segments of the body are dealt with. The proto- and deuto-cerebra are usually considered to be "acronal," though that term implies a subjective judgment concerning head metamerism. The tritocerebrum is derived from the first embryonic postoral segment. These comparisons are to imply analogies, though they may in part also produce homologies in some instances.

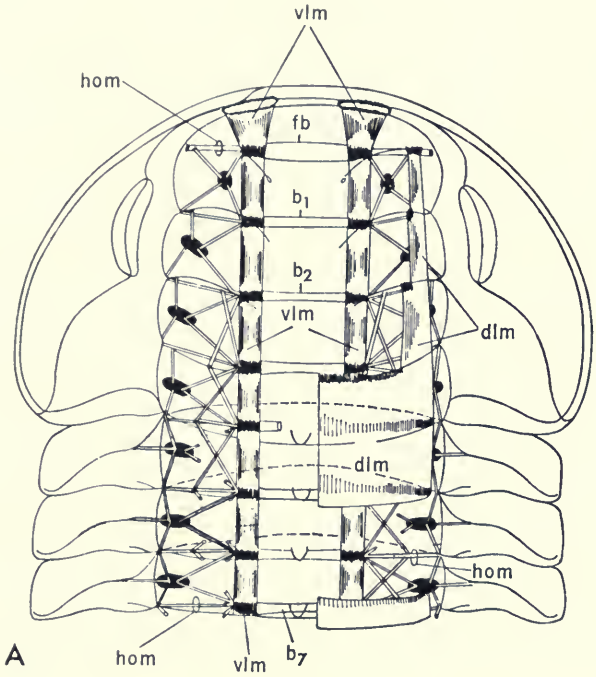
		Chelicerata	Pycnogonida	Crustacea	Onychophora	Myriapoda-Hexapoda	Trilobita
Preoral	protocerebral	—	—	—	—	—	—
	deutocerebral	—	—	antennule	antenna	antenna	—
	Tritocerebral I	chelicerae	chelifores	antenna	("lips")	(labrum)	antenna
postoral	II	pedipalps	pedipalps	mandible	mandible	mandible	1st leg
	III	1st leg	ovigers	maxilla I	slime papilla	maxilla I	2nd leg
	IV	2nd leg	1st leg	maxilla II	1st leg	maxilla II	3rd leg
	V	3rd leg	2nd leg	1st leg	2nd leg	1st leg	4th leg
	VI	4th leg	3rd leg	2nd leg	3rd leg	2nd leg	5th leg
	VII		4th leg	3rd leg	4th leg	3rd leg	6th leg
	VIII			4th leg	5th leg	(4th leg)	7th leg

all groups of arthropods. But Bullock and Horridge clearly point out the chelicerate chelae are tritocerebral in affinity, i.e., postoral in embryonic derivation. In all arthropod embryos the region forming the mouth and labrum moves posteriorly, while the lateral segmental tissue migrates forward. In addition, Cisne points out that, while he does not have any nervous system preservation in his fossils, the gut in his specimen travels some distance anteriad from the mouth and loops around *in front of all* the cephalic musculature, including that of the antennal segment (fig. 6). This structural arrangement would really seem to preserve the most primitive of arthropod states with little or no movement of any of the cephalic segments anteriorly during development, with only the mouth migrating posteriorly, the antenna and legs all being postoral in orgin. Linking this adult trilobite cephalic anatomy to the protaspid evidence presented above would indicate that the four segments of the late protaspid *are* postoral in position. It is very important to remember that the adult position of somite derivatives in relation to the arthropod mouth does not correspond to the relative position in the embryos. The condition of trilobites presented by me in Table 2 is thus based on Cisne's observations of trilobite internal anatomy, but is not his interpretation.

The pycnogonids have no deutocerebrum. The chelifores are supplied by nerves from the tritocerebrum which typically migrates from an embryonic postoral position to some forward location in the adult. This is a condition identical to that of the chelicerates. Wiren (1918) and Henry (1953) examined the *Nymphon* brain (fig. 7). In *Nymphon* a short circumesophageal commissure connects the large subesophageal ganglion with pedipalp and oviger nerves to the supraesophageal "brain," with the dorsal optic nerves and the anterior chelifore nerves.

Opposite:

FIG. 6. **A**, dorsal and **B**, lateral views of the head and first three thoracic segments of the trilobite *Triarthrus eatoni* showing the skeletomusculature and digestive system. A=antennal segment; b=post frontal endoskeletal bar; C=post antennal head segments; dlm=dorsal longitudinal muscle; e=esophagus; fb=frontal endoskeletal bar; fdm=frontal dilator muscle of esophagus (not seen but postulated); h=hypostome; hom=horizontal muscles; i=intestine; m=metastome; mca=mouth cavity; s=stomach; T=thoracic segment; tpa=tergal posterior apodeme; vdm=ventral dilator muscle of esophagus, vlm=ventral longitudinal muscle (modified from Cisne, 1974). Note that the esophagus is anterior to the frontal bar and the segmental structures related to the antenna.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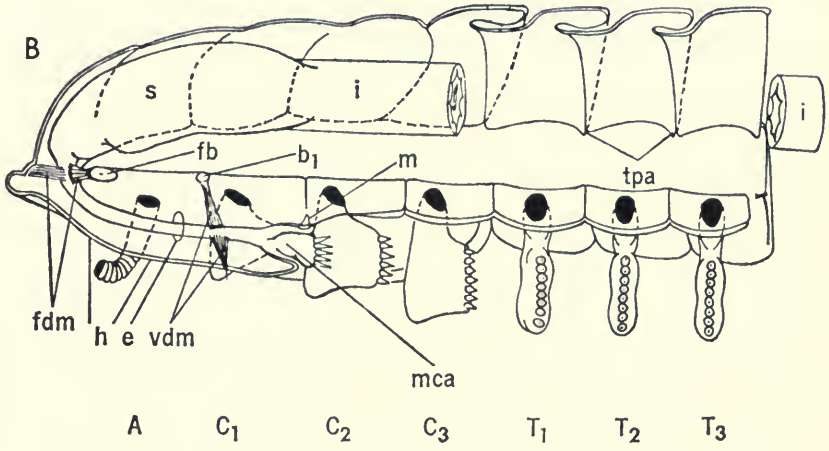
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Dissections by me of other pycnogonids reveal this arrangement can vary somewhat (fig. 7)[1]. *Dodecolopoda mawsoni* has a large subesophageal ganglion from which the pedipalp and oviger nerves arise (this ganglion is a fusion of the second and third postoral ganglia of the embryo), as well as paired nerves into the ventral part of the proboscis. The circumesophageal connectives are quite long and enshrine not only the esophagus, but a pair of proboscis levator muscles as well. This is a condition similar to that mentioned by Fry (1965). The chelifore nerves arise from the area where the commissures meet the brain.

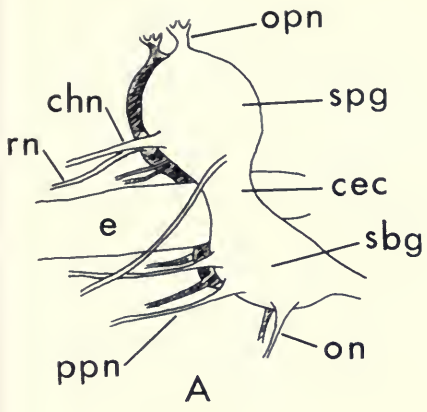
Colossendeis australis is similar in most respects to *Dodecolopoda*, except that in its final molting stage to the adult the chelifores are lost. The commissures in this species again encircle the esophagus and proboscis levators, but there is no chelifore nerve. The only indication of the former presence of this appendage is the chelifore diverticula from the gut which arise behind the commissures, come around lateral to them, and proceed anteriorly to the point where the base of the chelifore would have been. These gut diverticula dead end at the base of the proboscis.

This compression and movement of the interior ganglia forward is related to the distinctive location of the pycnogonid mouth. The mouth, unique among arthropods, is usually directed anteriorly as opposed to a primitive ventral or ventro-posterior orientation (Hessler and Newman, 1975). Both *Dodecolopoda* and *Colessendeis* display a compression of the ventral nerve ganglia toward the anterior end of the body. This is opposed to the condition that Henry (1953) observed in *Nymphon* where each ganglion was located at the level of the segment it served.

[1]Material supplied by Professor Joel W. Hedgpeth from his personal collection.

Opposite:

FIG. 7. Central nervous systems of pycnogonids. A, *Nymphon* sp. (modified from Wiren, 1918), brain and anterior nerves in relation to the esophagus; B, trunk ganglia of *Nymphon pixillae* (modified from Henry, 1953); C, trunk ganglia of *Dodecolopoda mawsoni;* D, brain and anterior nerves in relation to the head anatomy of *D. mawsoni*; E, brain and anterior nerves in relation to the head anatomy of *Colossendeis australis*; F, trunk ganglia of *C. australis.* spg=supraesophageal ganglion, sbg=subesophageal ganglion, cec=circumesophageal commissure, opn=optic nerve, chn=chelifore nerve, rn=rostral nerve, ppn=pedipalp nerve, on=oviger nerve, e=esophagus, chd=chelifore diverticulum, ppd=pedipalp diverticulum, ch= chelifore, pp=pedipalp, o=oviger, 1st wl=first walking leg, pr=proboscis, plm= proboscis levator muscle.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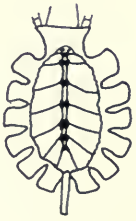

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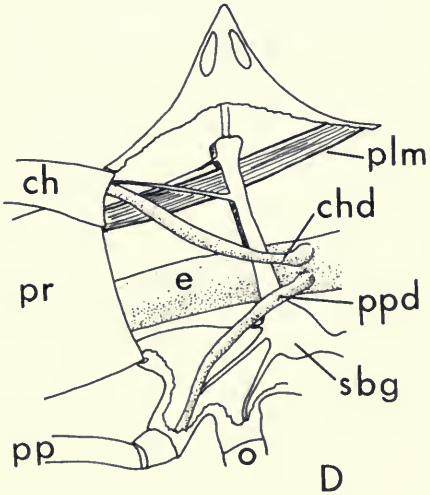
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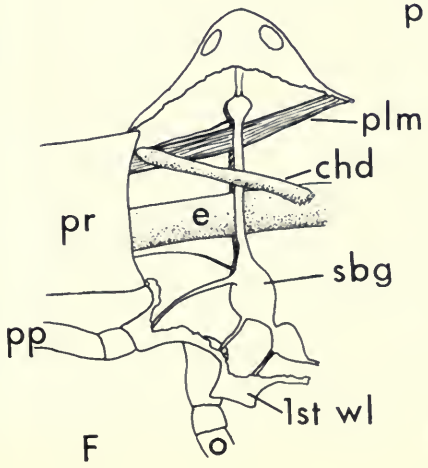
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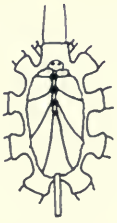

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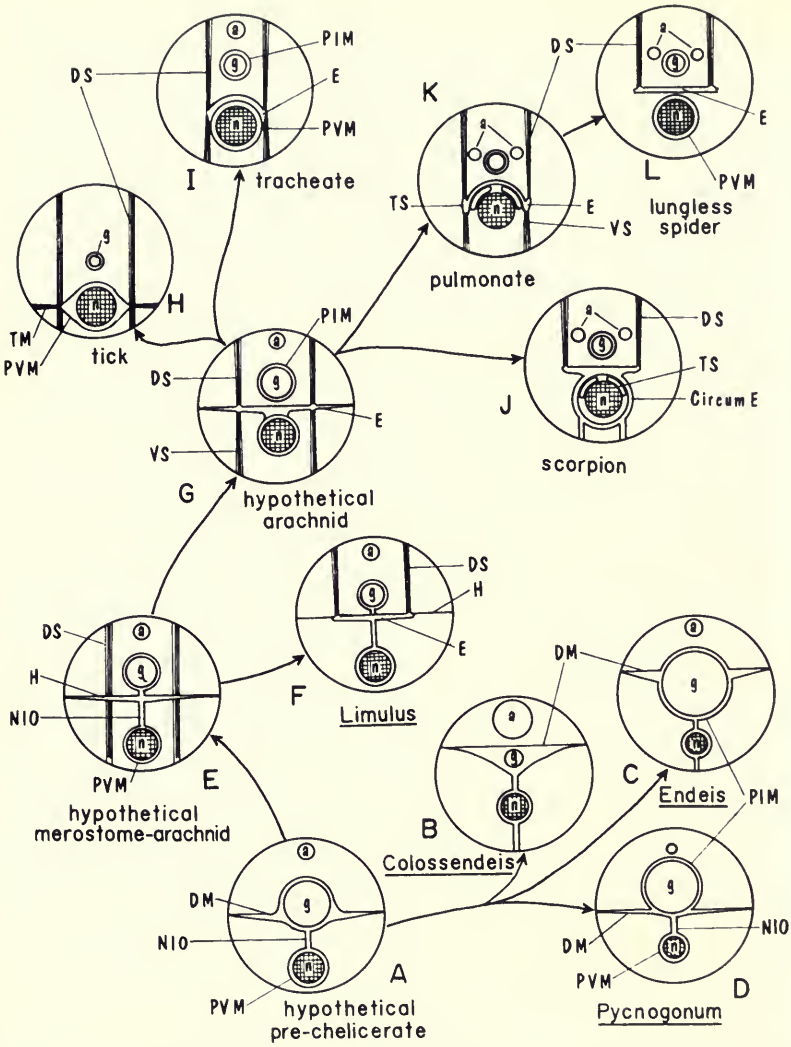

FIG. 8. Phyletic relationships of the Cheliceriformes (modified from Firstman, 1971), with cross-sections through the anterior trunk regions to display the relationships of Dohrn's membrane and the endosternites to the general trunk anatomy. **A**, hypothetical pre-chelicerate stage suggested by certain pycnogonids; **B**, Colossendeomorpha (*Colossendeis*); **C**, Nymphonomorpha (*Endeis*); **D**, Pycnogonomorpha (*Pycnogonum*); **E**, hypothetical ancestral merostome-arachnid; **F**, *Limulus*; **G**, hypothetical ancestral arachnid; **H**, tick; **I**, typical tracheate arachnid; **J**, Scorpionida; **K**, typical pulmonate arachnid; **L**, lungless spider. a=aorta, g=gut, n=central nervous system, DM=Dohrn's membrane, PVM=perineural vascular membrane, NIO=neural intestinal omentum, H=horizontal membrane, E=endosternite, VS=ventral suspensor muscle, DS=dorsal suspensor muscle, TM=transverse muscle, PIM=peri-intestinal membrane, TS=thoracic sinus.

LOCOMOTOR ANATOMY

The work of Manton has come to make the structure and function of arthropod appendages very important to the modern phyletic theory of the group. Not as much detailed analysis has been done on appendage morphology in trilobites, chelicerates, and pycnogonids as in the uniramians and crustaceans.

As mentioned above, Manton (1973a, b) considered the chelicerates. A divergent origin of this group from other arthropods was suggested by several factors. There was probably a small number of legs in the ancestral chelicerate form and thus no concomitant need for rigid co-ordination of gaits. There is a great importance to rocking movements in arachnids, with most limb joints being equipped with flexors and few extensors and only a limited promotor-remotor movement at one joint. Extension is achieved by regulating body fluid pressure (Ellis, 1944). The arachnid coxa is typically an immobile joint, while in the limulids the coxa is capable of a strong transverse action to engage the gnathobases during feeding as well as promotion-remotion. The origin of the chelicerates was thus different from that of the uniramians or crustaceans, both of which involved multi-legged, well co-ordinated types.

Firstman (1971) has demonstrated on the basis of gross dissections the importance of the endosternite derived from vascular membranes in chelicerates. This structure is unique to chelicerates and to some extent pycnogonids. It functions as a point of origin for locomotor muscles, serving as a free-floating skeleton anchored by body wall muscles which insert on it. It is derived from the mesodermal vascular membranes surrounding the gut and nerve chord. These membranes have become impregnated with connective tissue as they became associated with body muscles. The body wall muscles serve to tense the endosternite as the animals move. This system serves as a substitute for the apodemal (ectodermal) endoskeleton of uniramous and crustaceous arthropods which functions similarly. The endosternite is developed in inverse proportion to any apodemes that may be present, so that in the Order Solpugida an endosternite has been completely replaced by an extensive apodemal system. Firstman observes that the pycnogonids have a perivisceral sinus similar to the endosternal-associated sinus of chelicerates that lack booklungs. On this basis he associates the pycnogonids with the chelicerates (fig. 8).

There is a question as to whether the chelicerate limbs are primitively uniramous or biramous. The appendages of all chelicerates, living and extinct, are uniramous, except for some exceptions in *Limulus*. The sixth prosomal appendage of *Limulus* has a small lobe, the flabellum, attached to the dorsalmost projection of the coxa, and the respiratory appendages of the mesosoma have gills developed on the posterior surfaces of a rather broad, flat, laterally directed lobe. The significance of these structures is not clear. Størmer (1944) considered these as indications that the chelicerate limb was primitively biramous. He homologizes the flabellum and respiratory lobes of *Limulus* with the filamentous branch of the trilobite limb. Kaestner (1968) seems to have some reservations about such an interpretation for the respiratory appendages of the mesosoma, though he is not specific. The appendages of the Cambrian *Aglaspis* prosoma (the most primitive known chelicerates) are uniramous (Raasch, 1939). Only the first appendage is chelate and none of the aglaspid postoral appendages seem to have gnathobases (fig. 9). This might seem to indicate that the appendage morphology of the limulids may be quite specialized.

It is perhaps important to note that the flabellum occurs only on the one prosomal appendage, which, besides biting in a transverse plane, serves to push food forward into the anterior part of the *Limulus* food groove. The flabellum itself is directed back over the gill appendage chamber and may serve a special function in setting up respiratory currents. The respiratory appendages arise embryonically as a flap from which the medial, more distal elements of the limb develop. One might thus legitimately interpret the respiratory portion of the mesosomatic limbs as specializations of the coxa.

Little has been published on pycnogonid locomotory morphology except for some observations by Cole (1901), Prell (1911), Arita (1937), and Morgan (1971). Examination of preserved pycnogonids by me indicate that the movement in pycnogonid leg joints is very restrictive. The body-first coxa joint is almost immobile, capable of only slight dorso-ventral movement, if at all. The first coxa joint is the only one capable of promotion-remotion. All the other joints in the leg move dorso-ventrally. Viewing of movie film of various pycnogonids in motion reveals a great variety of gaits in pycnogonids (Schram and Hedgpeth, 1978). An extensive analysis is not possible here, but some generalizations can be made. 1) Pycnogonids typically execute rather inaccurate and unco-ordinated stepping movements, although there are some exceptions, such as *Deco-*

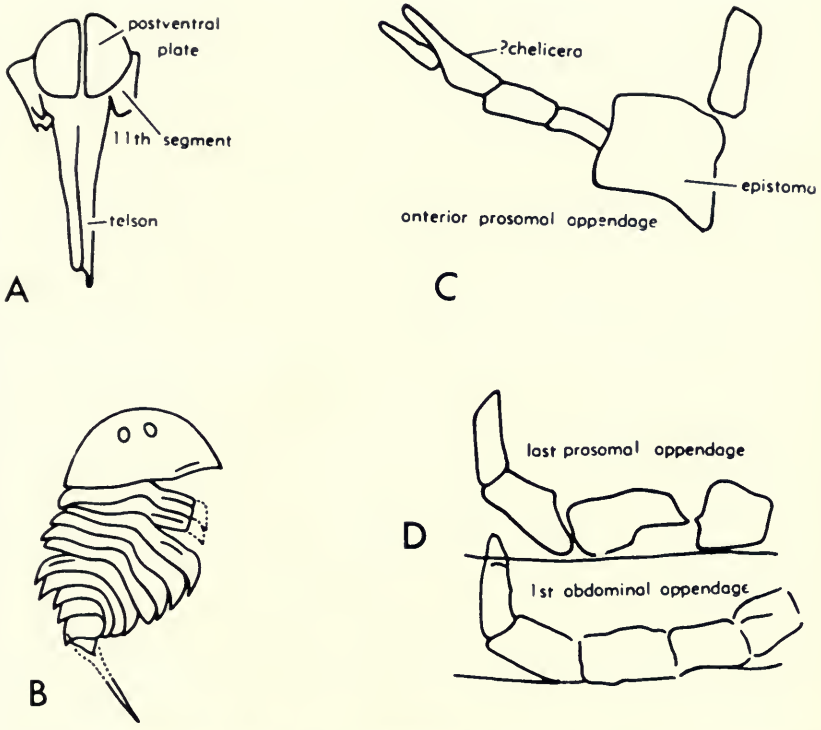

FIG. 9. Anatomical features of Cambrian aglaspids noting the uniramous character of the limbs. A, *Urarthrus instabilis*, posteriormost extremity from the ventral side; B, *Aglaspis spinifer*, whole body; C, chelate first prosomal appendage with epistoma of *A. spinifer*; D, last prosomal and first abdominal appendages of *A. spinifer*. From Størmer, 1955.)

lopoda which moves in a well co-ordinated manner. Others, e.g., *Colossendeis*, can be characterized as "stumbling about" when they move. 2) The promotor-remotor action is generally limited. Because of the arrangement of legs on a pycnogonid body in a radial configuration, the animals can sometimes move without any promotion-remotion depending on the direction of travel, and *Dodecalopoda* doesn't appear to use it at all. 3) The importance of the "rocking" pattern in individual leg motion (similar to that described above for chelicerates) is very marked, though in some forms it seems to be rather labored and deliberate. In general, pycnogonids seem to share many features in common with the chelicerate pattern of locomotion, such as "rocking," inaccurate stepping movements, and de-

emphasis of promotor-remotor action at a specific joint. This agrees with what is found in *Limulus* and arachnids. Terrestrial chelicerates do not have extensor muscles in some of the leg joints, but use fluid pressure to extend the leg, as may also be the case in pycnogonids. The segments of legs of at least some pycnogonids are not all equipped with extensor and flexor muscles.

Relatively little is known concerning trilobite limbs. Of the hundreds of trilobite genera, only six are known at all well (Størmer, 1939; Harrington, 1959). On this limited basis trilobites have often been characterized as having similar appendages. Though trilobite appendages are alike in general form, having a strong telopod and a "filamentous branch" arising from the coxa, an examination of these few species reveals a potential for a wide range of functional variations (fig. 10).

Olenoides (Whittington, 1975b), *Triarthrus* (Cisne, 1975), *Naraoia* (Whittington, 1977), and possibly *Cryptolithus* (Bergstrom, 1972; Campbell, 1975) possess medially directed spines or setae on the coxa which may have functioned like *Limulus* coxae, or possibly utilized a pushing action more like crustaceans. *Phacops* (Stürmer and Bergstrom, 1973), *Naraoia*, and *Cryptolithus* have spines and "gnathic" structures on more distal segments of the telopod. *Ceraurus* has a completely unadorned telopod, no "gnathic" structures at all. The morphology of the filamentous branch exhibits even more diversity (the use of terms like "preepipodite" or "exite" leads to phyletic and anatomical conclusions which are not necessarily justified). Bergstrom (1969) gives some convincing arguments against the filamentous branch being able to function in respiration. Bergstrom points out that the cuticle of the filaments is relatively thick. Though the filaments are flexible they do not collapse or fold as a structure with a thin cuticle would do, and the filaments are preserved equally as well as the trilobite telopod. This would seem to imply a cuticle on these filaments too thick to sustain a respiratory exchange of gases, though Whittington (1975b) seems to disagree. Bergstrom also raises a question about the mechanics of getting body fluid out into the filaments and back, and the ability of the trilobite body plan to sustain the necessary high body fluid pressure to achieve it. Bergstrom feels that the apparently thin cuticle on the underside of the trilobite pleura is a better candidate for the respiratory surface.

Cannon and Manton (1927) illustrate how the filamentous branch

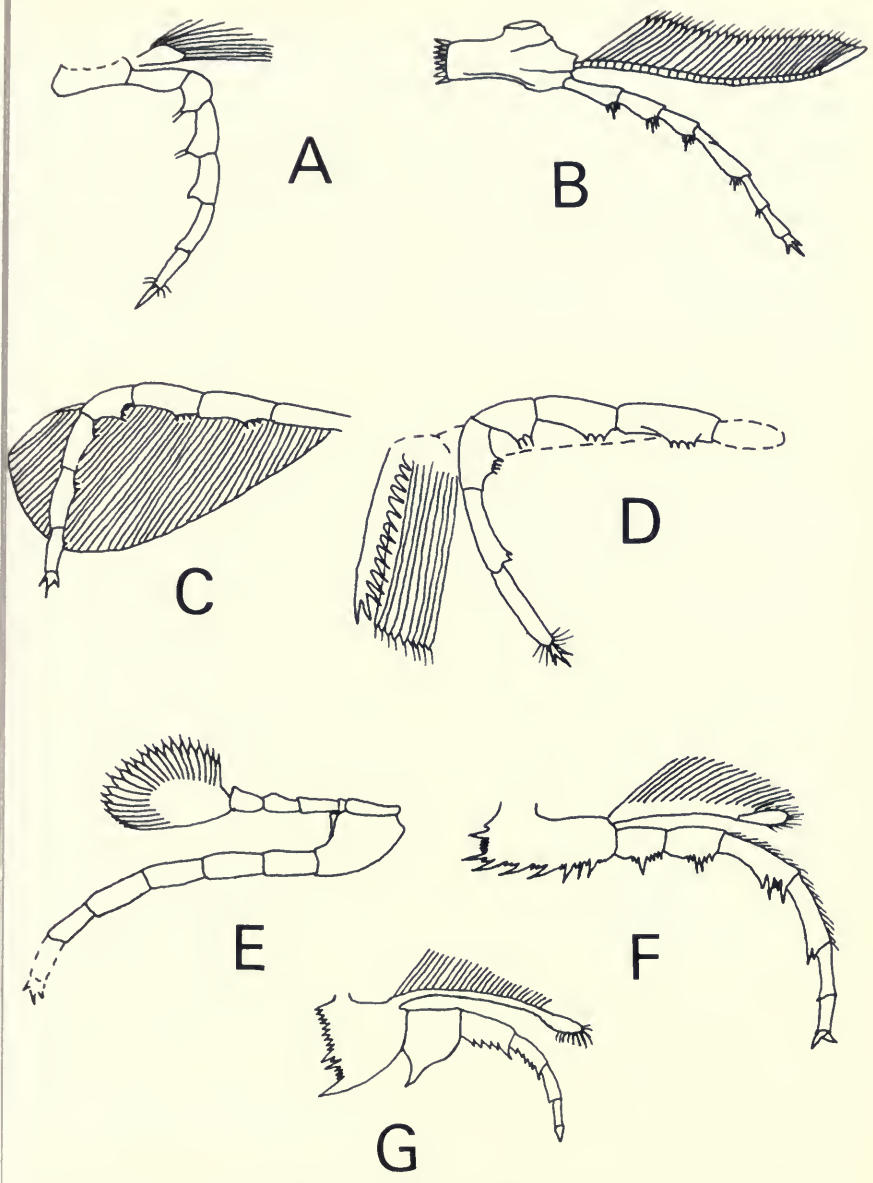

FIG. 10. Trilobite appendages. **A**, *Phacops*, anterior view (modified from Stürmer and Bergstrom (1973); **B**, *Triarthrus eatoni*, anterior view (from Cisne, 1975); **C**, *Cryptolithus tesselatus*, ventral view (from Campbell, 1975) **D**, *C. tesselatus*, ventral view (from Bergstrom, 1972); **E**, *Ceraurus*, anterior view (modified from Størmer, 1939); **F**, *Olenoides serratus*, anterior view (modified from Whittington, 1975b); **G**, *Naroia compacta* (from Whittington, 1977). Filamentous branches of A, B, E, F, and G actually extending into the plane of the figure.

can act as a device to set up a filter feeding current (see below). But Bergstrom (1972) discusses how the filamentous branch of *Cryptolithus* could have been used in a more "aggressive," non-filtering, feeding action. He suggests that in *Cryptolithus* the filaments are restricted to only the distal part of the filamentous branch and are directed downward. He believes these filaments were probably used to stir up sediments over which the animal walked. Campbell (1975) disagrees with this arrangement. Whittington (1975b) analyzed *Olenoides* tracks and trails and concluded their legs moved metachronally, and that the "filamentous branches" may have assisted in this.

FILTER FEEDING

Cisne (1973, 1975) stated that trilobites feed in the manner of cephalocarids and other primitive crustaceans. Marshall and Orr (1960) give four criteria for a filter feeder: 1) a filter; 2) a means of creating a flow of water through the filter; 3) some way of scraping the filter and getting the food to the mouth; and 4) an exit for the filtered water. Cannon and Manton (1927) and Barrington (1967) give some lucid accounts of various filter feeding devices. We need be concerned with only three types in this account (fig. 11).

The primitive crustacean filter feeding apparatus is composed of a series of superficially imposed, ventrally directed paddles (fig. 11G-I). This is the type found in the cephalocarids. On the forward stroke, the space between the paddles is increased and water is sucked up between the limbs. Food particles in the water are trapped on the setae of the limbs. On the backstroke the bulk of the water is pushed out from between the limbs in a propulsive stream, but a backwash current is created on the anterior surface of the paddles which carries a stream of water dorsally, helping to clean off the setae, and sweeping the particles into a midventral food groove. The action of the opposed coxal setae and the anterior current in the food groove created by the action of the hypostomal flap moves the food to the mouth. There it is trapped with the assistance of mucous secretions of the epistome and the maxillary setae.

It is difficult to compare any possible trilobite mode of filter feeding with the above crustacean type. Tiegs and Manton (1958) felt there might be some difficulty in attempting to oppose trilobite gnathobases, as in the chelicerates, or coxal setae, as in the Crustacea. Cisne (1975) and Whittington (1975b, 1977) reconstruct trilo-

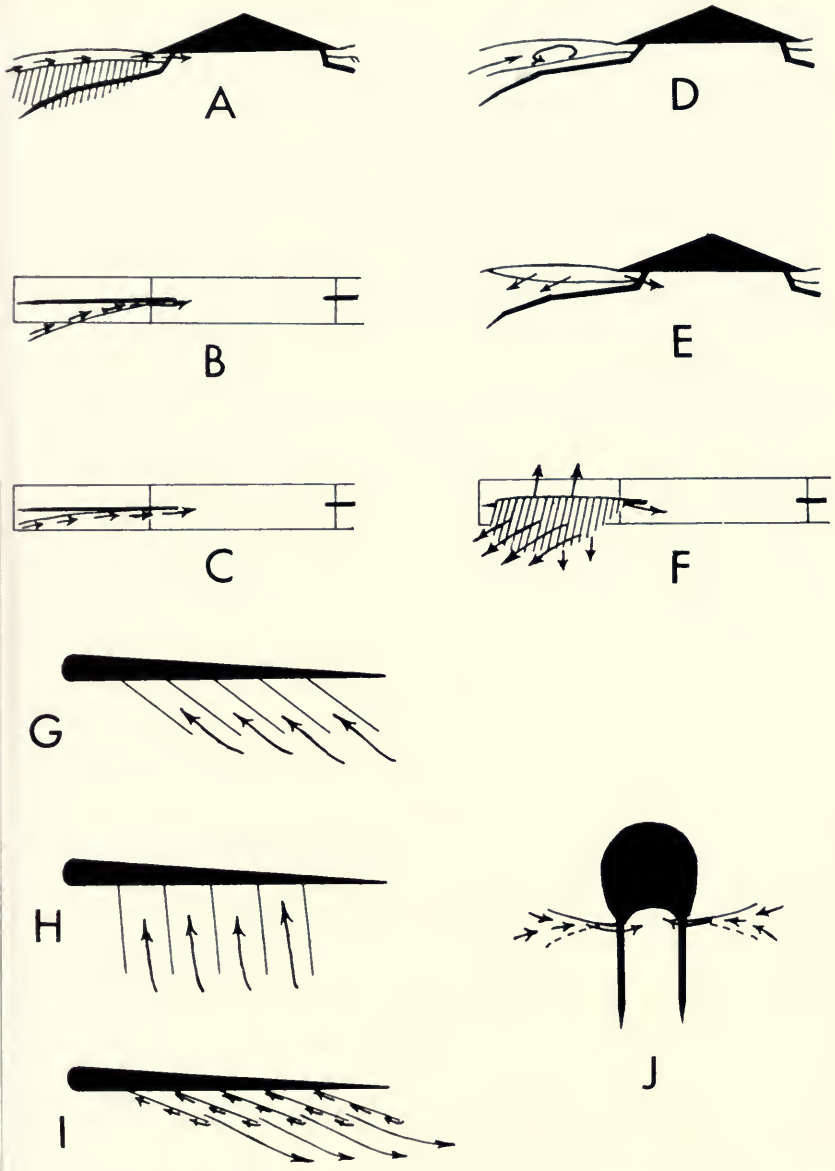

FIG. 11. A-C, Cannon-Manton hypothesis of trilobite limb function with A, cross-sectional view, and B and C, ventral views at successive stages (arrows indicate flow of water). D-F, Størmer hypothesis of trilobite limb function with D and E cross-sectional views at successive stages and F a ventral view of stage E. G-I, current flow around the limbs of a primitive crustacean type (lateral views). J, current flow around the functioning expodites of a mysid crustacean.

bite legs with opposed coxae. The ventro-laterally directed telopod of the trilobite is generally conceded to be a "walking" type of limb. The telopod may be supplementary to feeding if some of the segments of the leg can function as subchelae, e.g., *Cryptolithus* or *Olenoides*. The only structure on the leg that apparently can function in filter feeding is the laterally directed filamentous branch. Cannon and Manton (1927) thus proposed a different mode of filter feeding in the trilobites from that of crustaceans (fig. 11A-C). They noted the filamentous branch is placed parallel to the pleura. The only way this might function to set up a feeding current is if the branch vibrated back and forth, the filaments directed ventrally. This vibration under the rigid pleura would serve to set up a backwash current along the dorsal edge of the filamentous branch, moving water medially. Tiegs and Manton suggest a large labrum or hypostome, e.g., like that seen in the remopleurids, combined with the action of the pharynx must have served to create a suction to pull the food current forward. But the form of the trilobite hypostome varies from the very small, e.g., *Dimeropyge*, to quite large, implying that the hypostome might not have functioned similarly in all trilobites.

Størmer (1939) postulated a different use of the filamentous branch to set up a feeding current. In his analysis of the filamentous branches or *Cryptolithus* he noted that they seemed to be arranged so that the filaments were directed posteriorly, i.e., were parallel to the pleura (fig. 11D-F). He assumed all trilobites were so oriented. When the filamentous branches were depressed ventrally, they would suck in a volume of water into the subpleural space. Størmer then postulated that when the filamentous branches were raised so that the distal tips touched the pleura, closing off the subpleural space, this would force water forward toward the mouth. However, it appears to me that this elevation would not only force water forward, but also ventrally through the filaments, medially between the leg bases, and posteriorly. Furthermore, when the filamentous branches would be depressed to allow more water to flow into the subpleural space, all the currents set up by the elevation, including the one moving forward toward the head, would be broken by turbulent flow induced by the depression. The main defect of the Størmer hypothesis is that it does not allow for separate currents, one for getting food and the other for moving it to the mouth, as does the Cannon-Manton scheme. The Cannon-Manton hypothesis seems to be the most functionally feasible.

Thus the trilobite mode of feeding would be different than that of the primitive crustaceans, like *Hutchinsoniella*, and is only remotely similar to that found in the "schizopodous" malacostracans, those with "biramous" thoracic limbs (fig. 11). In this latter group the exopod of the leg is directed laterally and somewhat posteriorly and rotated in a circular pattern to describe a cone. A vortex, created up the center of the cone, directed medially, directs a feeding current into a midventral food groove. The arrangement of the leg components help direct the current forward and the action of the maxillary setae assist in capturing the food particles as the food stream passes through them.

Cannon and Manton suggest that if one wishes to relate them, all of these types of filter-feeding mechanisms could be only derived from some strictly hypothetical form.

BI- AND POLYRAMOUS APPENDAGES

A kind of convergence exists in the appendage structure of trilobites and malacostracous crustaceans; both exhibit a biramous condition. The oft-quoted similarity here, though, is superficial and the phyletic import attached to this is minimal. The exite-like filamentous branch of trilobitomorphs arises from a basal segment (a coxa or precoxa) of a seven- or eight-segment telopod, while malacostracans have a two-segment leg base off which can arise exite gill flaps, a filamentous exopodite, endites, and a telopodic-like endopod of five segments. Though the two main branches of the eumalacostracan limb lend it a biramous character, the wide array of possible endite and exite structures betray its polyramous ancestry.

Similarity between crustacean and trilobite limbs disappears when the *primitive* crustacean limb type is examined (fig. 12). Borradaile (1926) was the first to point this out and the recent work of Sanders (1963) and Hessler (1964) on cephalocarids reinforces these considerations. (Indeed, I would recognize three basic limb types in arthropods: the uniramous telopods of uniramians and chelicerate-pycnogonids; the biramous type of the trilobitomorphs; and the polyramous, foliaceous type of the crustaceans.) The basic crustacean limb, as illustrated by the trunk appendages of cephalocarids, is thin and leaf-like, composed of a basal protopod off which arises a flap-like epipodite; a foliaceous exopod; a weakly telopoditic endopod; and several endites (fig. 12). This foliaceous limb can best be

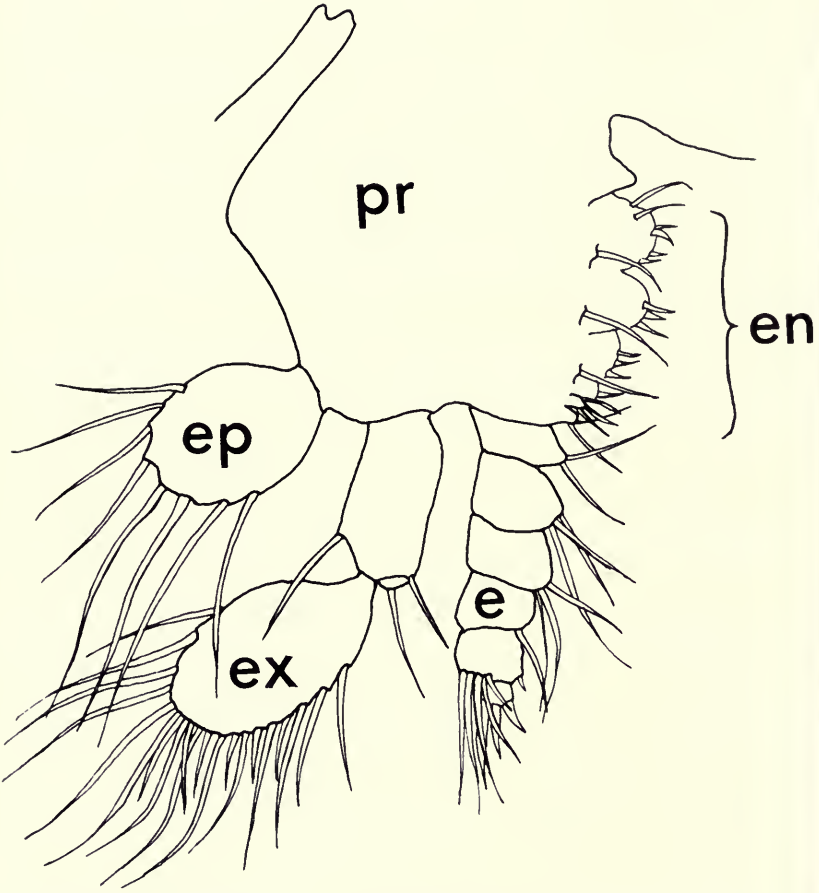

FIG. 12. Thoracic limb of the cephalocarid crustacean, *Hutchinsoniella macrocantha*. pr=protopod, ep=epipodite, ex=exopodite, e=endopodite, en=endites.

termed polyramous. The number of exites and endites that can be developed on this basic form in different crustacean groups is various. This plan is elaborated upon in the course of the crustacean radiation in the branchiopods, ostracods, many of the maxillopodans, and the primitive malacostracans. It is only in the higher malacostracans and the cirripeds that there is a deviation from this plan (fig. 13).

Any similarity, as stated above, between the trilobite biramous limb and that of the higher crustaceans is purely convergent. The convergence arises from the functional similarities the parts of the

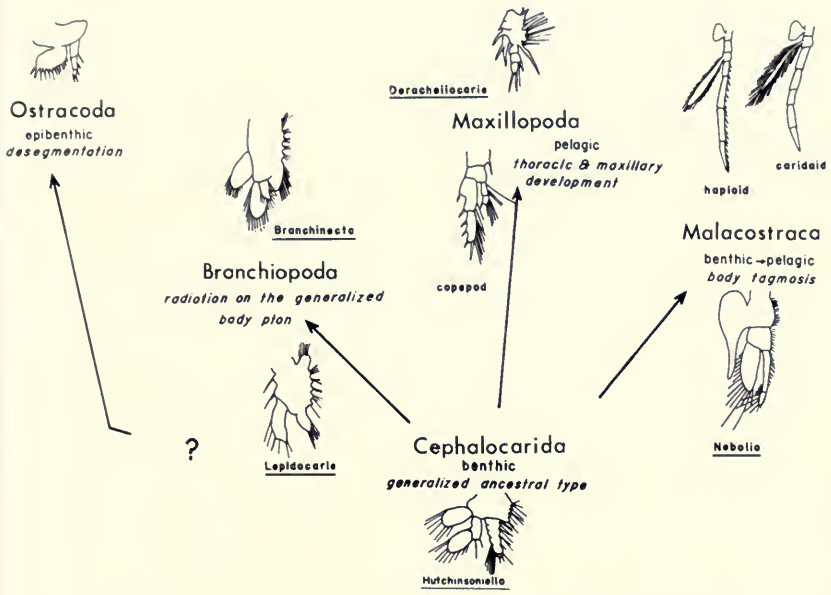

FIG. 13. Phyletic relationships of the classes of Crustacea with the ancestral environment and main anatomical exploitation of each class given. Representative thoracic appendages illustrate modifications and variations which can take place on the ancestral type.

limbs share. The trilobite telopod and the malacostracan endopod are walking or pushing structures which require their long, cylindrical, well-muscled arrangement to develop motive power. The trilobite filamentous branch and the schizopod exopod are swimming and sometimes filtering elements.

BODY MUSCULATURE AND TAGMATA

Cisne (1974) points out the marked similarity of trilobite body muscles and those of cephalocarids (Hessler, 1964). But it is also interesting to note the similarity of these to other arthropods, e.g., the musculature of chilopods (Manton, 1965). Though these similarities are interesting, the possibility of convergence must again be raised. Schram (1969) has already indicated a convergent development in the complex "caridoid" musculature of hoplocaridans and eumalacostracans.

Cisne also discovered remnants of the liver and its diverticula in *Triarthrus* cephalon. The trilobite thorax apparently carried only

the hindmost portions of the gut toward the anus. In this regard the trilobite cephalon is more akin to the chelicerate prosoma than the typical crustacean cephalon, and the trilobite thorax-pygidium is thus more like a chelicerate opisthosoma than a crustacean thorax and abdomen. The cephalocarids, however, have a pair of simple diverticula from the anterior midgut extending forward into the cephalon (Hessler, 1969).

TRILOBITE PHYLETIC AFFINITIES

The separate and distinct nature of Uniramia, Crustacea, and Chelicerata seems to be well established on the basis of embryology and leg morphology. What then are the possible phyletic affinities (table 3) of the Trilobitomorpha and the Pycnogonida?

In this regard it should be noted that much information is coming to light in the restudy of the Middle Cambrian Burgess Shale trilobitomorphs under the direction of Prof. Whittington and his colleagues at Cambridge (Whittington, 1971, 1974, 1975a, 1977; Hughes, 1975). These trilobitomorphs were generally thought to possess trilobite-like limbs but exhibit a variety of body forms. The actual trilobite radiation is basically an elaboration of one particular body type. Analysis seems to be indicating a great trilobitomorph radiation in the earliest Paleozoic, whose taxonomic affinities may be with many arthropod groups, i.e., not all trilobitoids may be related to trilobites.

Trilobites have characters that relate them to different groups depending on the selection. The only really sound crustacean similarities with trilobites lies in the nature of the body musculature and in both possessing anamorphic development. But there is a possibility of convergence in the muscle structure. Generally similar modes of habit might be expected to produce a similarity in musculature. The distinct nature of the basic appendage types and differences in the larval postoral segmentation in the two groups seems to preclude any relationship.

There are a few trilobite similarities with chelicerates: the restriction of the hepatic organs to the cephalon, the possession of four postoral segments in the protaspid larval stages, and possibly biramous appendages. These characters would seem to be stronger than those which relate trilobites to crustaceans. It is quite possible the hepatic location could be convergent. The embryonic evidence is perhaps significant, though there must always be an element of

TABLE 3. Character states of trilobites compared with the three living phyla of arthropods. Items indicating similarity (PROS) are commented upon: +=good point, c=possibly convergent, ?=not readily evaluable, g=general arthropodous character in primitive forms. Items arguing against affinity stated under CONS.

	PROS	COMMENTS	CONS
Uniramia	Multi-legged	+	Biramous appendages uniramous
	Homonomous	g	
Cheliceriformes	Cephalic hepatic diverticula	c	No endosternites
	Four postoral larval segments	?	1st embryonic postoral appendage as antenna rather than chelate
	(Biramous legs)	???	
Crustacea	Body muscles	c	Biramous appendages *vs.* polyramous
Unique	Body form (lateral pleurites)	+?	
	Biramous appendages	+	
	Function of leg parts in feeding	+	
	1st embryonic postoral appendage as antenna	+	

doubt since we can never be sure of what we are actually dealing with in the trilobite larva (unless someone comes up with a fossilized trilobite germinal disc). Trilobites, however, exhibit anamorphic development, while chelicerates are epimorphic. The supposed biramous nature of the chelicerate limb can only be doubtfully assessed, especially in view of what little is known of the most primitive merostomes, the Aglaspida. (Raw (1957) allies chelicerates and trilobites based on a detailed analysis of gross external morphology of the dorsal exoskeleton of olenellids. His analysis, however, is an excellent example of the opening quotation of this paper from Manton—unsound comments based on imprecise knowledge of the meaning of animal shapes.)

Trilobitomorph affinities to uniramians seem to be expressed only in that both are primarily multi-legged, homonomous forms. But their legs are not at all similar nor are their modes of feeding, and these among other factors seem to preclude any relationship.

There are some totally unique trilobitomorph characters. These are: the body form with great lateral development of the pleura, the biramous structure of the leg, the possible mode of feeding either as a filter feeder or any other suggested modification thereof, and the first postoral limb as an antenna. The body form is distinctive in the trilobites proper, but it should be noted that some of the Cambrian trilobitomorphs exhibit deviations from this form. The leg structure and function is most important both in its being quite distinct from any other arthropod types and in the importance that Manton has placed on limb functional morphology in separating arthropodous groups.

Important potential lines of evidence relevant to trilobitomorph affinities, such as brain structure, nerve innervation patterns, and early embryonic details will probably never be known. The evidence available at present indicates to me that establishing trilobitomorph relationships with uniramians and crustaceans is difficult, but, on the other hand, possible with chelicerates. Trilobitomorphs really appear to be rather unique, especially when judged on criteria similar to those used by Manton to set off the other arthropodous phyla. Thus a separate phylum, Trilobitomorpha, is suggested for these forms for the time being.

PYCNOGONID PHYLETIC AFFINITIES

Attempting to determine pycnogonid phyletic affinities has always posed a problem (table 4), partly due to a real neglect in at-

TABLE 4. Character states of Pycnogonida compared with the other groups of living arthropods. Items indicating similarity (PROS) are commented upon: +=good point, c=possibly convergent, (c)=slight chance of convergence. Items arguing against affinity stated under CONS.

	PROS	COMMENTS	CONS
Uniramia	Proboscis (protrusive lips of onychophorans)	c	Few legs on body
	Ventral organs	+	
Chelicerata	1st appendage chelate	c	
	Four postoral initial embryonic segments	+	
	Endosternites	+	
	Uniramous leg	+ (c)	
	Leg function in locomotion	+ (c)	
	No deutocerebrum	+	
	Liquid-suctorial feeders	c	
Crustacea	"Caprellid" form	c	Uniramous legs No deutocerebrum
Unique	Anterior mouth orientation	+	
	Body form	+	

tempting to gather information on their basic biology. They have been allied to every major taxon of arthropods at one time or another. Tiegs and Manton (1958), albeit only half seriously, suggested that they might be related to onychophorans. They compare the pycnogonid proboscis to the lips of *Peripatus* which can be extruded over the jaws. They also note that the ganglia of both pycnogonids and onychophorans develop from ventral organs in the embryo.

Nothing seems to relate the pycnogonids to the crustaceans. The body form of some pycnogonids is generally similar to that of caprellid amphipods or certain asellote isopods, but this is almost certainly due to a similarity of epizoic habit. This reflects part of the

problem with pycnogonids in general. They are undoubtedly a very ancient group which has become highly specialized to a particular mode of life.

There are several chelicerate-like characters possessed by the pycnogonids: first limb being chelate, four postoral segments in the earliest embryonic phases, endosternite similarities, similarities in the structure and function of the uniramous legs, liquid suctorial feeding habits, and the lack of a deutocerebrum. All these items seem to be very telling. The nature of the embryonic segmentation is quite interesting, but its full significance can be better evaluated when the earliest embryonic conditions of the pycnogonids are more fully understood. The limited promotor-remotor movement of the legs and the importance of the rocking movement of the appendage are most reminiscent of conditions seen in various arachnids. The liquefaction-suctorial mode of feeding in both pycnogonids and chelicerates is, given other anatomical features, startling, though possibly convergent.

Unique pycnogonid characters are the mouth orientation and, to some extent, the body format. On this last point, Lehman (1959) has shown that the Devonian pycnogonid, *Palaeoisopus problematicus*, had a multi-segmented abdomen. The pycnogonid abdomen or metasoma has thus been lost in the course of evolution of this group.

Looking at all the available evidence, it would appear that the pycnogonids have a strong connection with chelicerates proper. Some of the characters joining these groups could be convergent, but I feel this is an instance where the numbers of similarities are so high and of such a nature as to be more easily explained by postulating actual relationship rather than invoking multiple convergences, especially with other unquestioned characters uniting the groups (Schram and Hedgpeth, 1978). The pycnogonids are, however, probably a very early offshoot of the line leading to Chelicerata: a separate subphylum status for Pycnogonida should be maintained within a phylum Cheliceriformes, separate from the subphylum Chelicerata.

SUMMARY TAXONOMY

A summary taxonomy for the arthropodous phyla is presented here. It is understood now that the arthropodous condition is a grade of organization similar in character to a pseudocoelomate, or a lophophorate, or any other grade. If one does not wish to abandon

monophyly, then each of the phyla in this outline might be considered a subphylum, and the subphyla as superclasses.

Phylum: Uniramia, Manton, 1973
- Subphylum: Onychophora Grube, 1853
- Subphylum: Myriapoda Latreille, 1796
  - Class: Chilopoda Latreille, 1817
  - Class: Diplopoda Gervais, 1844
  - Class: Symphyla Ryder, 1880
  - Class: Pauropoda Lubbock, 1866
  - Class: Arthropleurida Waterlot, 1934
- Subphylum: Hexapoda Latreille, 1825
  - Class: Protura Silvestri, 1907
  - Class: Collembola Lubbock, 1862
  - Class: Diplura Börner, 1904
  - Class: Thysanura Handlirsch, 1908
  - Class: Pterygota (Insecta) Brauer, 1885

Phylum: Crustacea, Pennant 1777
- Class: Cephalocarida Sanders, 1955
- Class: Branchiopoda Latreille, 1817
- Class: Ostracoda Latreille, 1806
- Class: Maxillopoda Dahl, 1956
  - Subclass: Copepoda Milne-Edwards, 1840
  - Subclass: Mystacocarida Pennak and Zinn, 1943
  - Subclass: Branchiura Thorell, 1864
  - Subclass: Cirripedia Burmeister, 1834
- Class: Malacostraca Latreille, 1806
  - Subclass: Phyllocarida Packard, 1879
  - Subclass: Hoplocarida Calman, 1904
  - Subclass: Eumalacostraca Grobben, 1892
    (Several superorders)

Phylum: Cheliceriformes, nov.
- Subphylum: Pycnogonida Latreille, 1810
- Subphylum: Chelicerata Heymons, 1901
  - Class: Merostomata Dana, 1852
    - Subclass: Xiphosura Latreille, 1802
    - Subclass: Eurypterida Burmeister, 1843
  - Class: Arachnida Lamarck, 1801

Phylum: Trilobitomorpha Størmer, 1944
Class: Trilobitoidea Størmer, 1959
Class: Trilobita Walch, 1771

ANCESTRAL TYPES

To some extent the question of whether a taxon is polyphyletic or monophyletic is semantic. It depends on where one wishes to "draw the line." In the context of the present discussion, it is sufficient to state that *if* the "phyla" in question cannot be derived from an *immediate* common ancestral type, they are polyphyletic. Naturally, one could continue to postulate ancestral, hypothetical types and eventually draw all the divergent arthropodous strains together to some "segmented worm." Each of those hypothetical intermediates, however, must be considered as an "arthropod." One could do this, but the end product would be a rather extensive "paper phylogeny" for which there would not be any concrete evidence. Manton (1973b) has laid down an important tenet or law of phylogeny which is implicit in all her work. Every stage in a postulated series connecting one morphological form with another *must be* completely functional in all its aspects. To postulate going from a stage A to stage B via any stages which are functionally impossible is not allowable. Profound differences of embryology and locomotory morphology in the end points of the clade must be reconciled.

Therefore, when I delineate ancestral types for the various arthropodous phyla, I am merely elucidating forms which could have given rise to the "phylum" in question and not making comment on what might have preceded such stages. Speculations along these lines (e.g., Melnikov, 1971) are interesting, but do not easily lend themselves to functional proof.

We might now delineate a possible ancestral condition for each arthropodous group adding to the initial efforts of Manton (1973a, b) in this regard.

The Uniramia are evolved from a form characterized as multi-legged, with a soft body, with lobopodial limbs, manipulating food (incipient biting) with the tips of the future jaws, omnivorous in diet, with a basically annelidan embryonic pattern, and at least initially epimorphic development.

The Crustacea have evolved from a form that was multi-legged, having polyramous and foliaceous appendages, manipulating food

with the base of the future jaw, a filter feeder, with a "crustaceoid" embryonic pattern, and at least initially anamorphic development.

The Cheliceriformes are evolved from a form with relatively few legs with possibly uniramous lobopodial limbs, possibly manipulating food with several leg bases with the assistance of some limb tips, carnivorous in diet, with "cheliceriform(?)" yolk-modified embryonic pattern, and epimorphic development.

The Trilobitomorpha are derived from a form that was multilegged, with biramous appendages, a detritus feeder, an unknown embryonic pattern, and anamorphic development.

CONCLUDING REMARKS

Certain monophyletic sensibilities may be offended by recognizing four arthropodous phyla. The establishment of the concept of arthropods as a convergent phenomenon is based on more than just gross anatomy with little or no reference to function or any other aspects of the biology of the animals. To quote Manton (1973b, p. 317), "The evidence of comparative functional anatomy and habits of life has thrown more light on the course of evolution and their directing forces than has any other type of evidence, and an immense mass of hitherto meaningless structure has become intelligible." This points out the fact that when we describe a taxon, at no matter what level, we cannot deal exclusively with gross anatomy as if in a vacuum. We must of necessity look at all the aspects of the living system insofar as is possible. This must of necessity include anatomical, functional morphologic, genetic, ecologic, geographic, biochemical aspects of an *entity*, rather than what we have come to be satisfied with when we have heretofore described a *taxon*.

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